

# Temporal and spatial variability among grazers: variability in the distribution of the gastropod *Cyphoma gibbosum* on octocorals

Howard R. Lasker<sup>1</sup>, Mary Alice Coffroth<sup>2,\*</sup>

<sup>1</sup> Department of Biological Sciences, State University of New York at Buffalo, Buffalo, New York 14260, USA

<sup>2</sup> Division of Biology and Living Resources, Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Cswy, Miami, Florida 33149, USA

**ABSTRACT:** Censuses of the gorgonian grazing gastropod *Cyphoma gibbosum* were conducted at 3 sites in the San Blas Islands, Panama, during the summers of 1981 to 1986. Snail density at the sites varied as much as 6-fold between years and sites. The most commonly occupied gorgonians were *Pseudopterogorgia* spp., *Plexaura homomalla* and *Pseudoplexaura* spp. They were occupied by snails in numbers disproportionate to the gorgonian's abundances. *C. gibbosum* exhibited significant clumping in their distribution on colonies. Most individuals exhibited strong preferences for a single species or in some cases for a single gorgonian colony. Snails observed over multiple years often switched preferences between years. Individual preferences, the movement of different snails through the study sites, and the formation and breakup of aggregations created significant temporal variability in observed preferences. Even greater levels of variation in preferences were present in distribution data collected during single visits to reefs at 17 sites throughout the Caribbean. Preferences at these sites as well as other published accounts only weakly support the preferences observed in the San Blas. *Pseudopterogorgia* spp. were most often preferred but at only 29% of sites. Data suggest that *C. gibbosum* distribution patterns are controlled by a combination of species preferences and social behaviors which lead to aggregated distributions. The combination of effects leads to distribution patterns which mask overall preferences and which may bias short-term observations. When examined over longer periods and/or across multiple sites a pattern emerges in which snails are distributed among a combination of actively preferred and randomly chosen species. Thus the distribution pattern is driven both by differences among host species and by stochastic processes. Recognition of these different mechanisms of host choice will be important in predicting the effects of grazers like *C. gibbosum* on their prey populations.

## INTRODUCTION

Grazers are capable of controlling the abundance of a wide variety of marine benthic algae and invertebrates (Ogden et al. 1973, Sammarco et al. 1974, Glynn 1976, Lubchenco 1978, Hay 1981, Lubchenco & Gaines 1981, Lewis 1986). The potential importance of grazers has focused a great deal of attention on factors affecting their preferences. However, the effects of grazing on the structure of marine benthic communities is dependent not only on the preferences exhibited by grazers but also by variability in these prey preferences and by variability in the grazer's abundance.

Variation in the foraging behavior of marine benthic grazers has been related to both prey and grazer densities. For instance crown-of-thorns starfish *Acanthaster planci* prey preferences may be related to the density of coral colonies (Ormond et al. 1976, but see also Potts 1981). Similarly, predator density can also have a density-dependent effect on foraging. Bernstein et al. (1981) have attributed changes in the foraging of sea urchin *Strongylocentrotus droebachiensis* to such a density-dependent change in behavior. Individuals of species whose foraging is density dependent can appear to have strong preferences at any one time, but the effects of these species on community structure may be very different from the effects of specialist grazers.

Changes in grazer density over both time and space

\* Present address: Dept of Biological Sciences, State University of New York at Buffalo, Buffalo, New York 14260, USA

can also alter the importance of grazing in structuring benthic communities. Some of the best examples of these effects are (1) those created by the local distribution of grazers (Lubchenco 1978), (2) those caused by geographic variation in grazer densities (Estes et al. 1978, Hay 1984), and (3) those resulting from dramatic fluctuations in grazer density (Potts 1981, Scheibling 1986, Hughes et al. 1987). Given the potential significance of variations in prey preference and grazer density, assessment of this variation may be as important in determining grazer effects as assessment of central (i.e. overall) tendencies.

In this paper we examine variability in the behavior of the gorgonian-eating snail *Cyphoma gibbosum* and show how individual, temporal, and spatial variability create a diversity of observed grazing patterns. *C. gibbosum* feeds exclusively on gorgonians. However, different authors have reported different prey preferences and some have found no preferences at all (Kinzie 1970, 1974, Birkeland & Gregory 1975, Hazlett & Bach 1982, Harvell & Suchanek 1987). Kinzie (1970) found the distribution of snails on gorgonians mirrored species abundances on the reef at Discovery Bay, Jamaica, and he failed to find any prey preferences in choice experiments between *Briareum asbestinum* and other species. In contrast, Birkeland & Gregory (1975) reported that *C. gibbosum* were found preferentially on *Gorgonia* spp. and *Eunicea succinea*. They found that *C. gibbosum* chose *Gorgonia* spp. over other species during in situ experiments. Harvell & Suchanek (1987), working at Salt River Canyon, St. Croix, US Virgin Islands, found that colonies occupied by *C. gibbosum* were a random subset of the gorgonian fauna. They did find that snails remained significantly longer on a mixed group of plexaurids which they identified as the *Plexaura* group (*P. flexuosa*, *P. homomalla* and *Pseudoplexaura crucis*). Finally, Lasker et al. (1988) found preferences for *Pseudopterogorgia* spp., *Pseudoplexaura porosa* and *Plexaura homomalla* at 3 sites in the San Blas Islands, Panama. The range of results reported may reflect sampling variation, or temporal and geographic differences in preferences, and/or prey quality. Although these effects are not mutually exclusive, it is essential that they be characterized before seeking explanations of observed prey preferences or predicting the effects of *C. gibbosum* grazing on gorgonian communities.

## METHODS

Three types of data were used in this study. Firstly, long-term data on the distribution of *Cyphoma gibbosum* on gorgonians at 3 sites in the San Blas Islands, Panama, were used to assess temporal variation in *C. gibbosum* abundance and distribution. Sec-

ondly, data on the movements of 244 marked snails were used to characterize variation in the distribution patterns of individuals as well as small-scale geographic variation in the San Blas Islands. Finally single-visit surveys of 17 sites located on 5 different Caribbean islands are used to characterize broader-scale geographic variation.

The work from the San Blas Islands was conducted at the facilities of the Smithsonian Tropical Research Institute. Observations of *Cyphoma gibbosum* feeding were made at 3 small patch reefs located within several kilometers of San Blas Point. The first reef, Macaroon, is a 50 × 30 m hardground in 3 to 4 m water. The fauna is dominated by plexaurid gorgonians, most notably *Pseudoplexaura porosa*. The second reef, Korbiski, is a large reef and reef-flat complex. The Korbiski study site was located in an area of mixed hardground and sand 1.0 to 2.5 m in depth at the northeast tip of the reef. The gorgonians *Plexaura* A (see Lasker 1984 for species description), *P. porosa*, *Plexaura homomalla* and *Plexaura flexuosa* were common at this site. The third reef, Pinnacles, is an area of mixed sand and hardground substrate with scattered clumps of hard coral. The site chosen for the study was a gently sloping area of sand and coral substrate at 5 to 7 m depth. The gorgonians *P. porosa* and *Eunicea* spp. were the most common species at Pinnacles. The 3 sites are described in greater detail in Lasker et al. (1988).

Censuses of *Cyphoma gibbosum* were conducted within arbitrarily selected 100 m<sup>2</sup> areas at each site. The areas were marked and a grid laid out at 2 m intervals. All colonies within the 10 × 10 m areas were identified to genus and/or species, and those which were visited by *C. gibbosum* were tagged and mapped. Censuses were conducted at Korbiski during July 1981 and at all 3 sites during June–July 1983 and January 1984. During these censuses the number of snails present and the identity of the prey species were recorded. More detailed monitoring at the sites was conducted during 1984 (8 Jun to 8 Aug), 1985 (6 Apr to 26 Jun), and 1986 (7 Jun to 19 Jul). During 1984 and 1985 all the sites were searched for *C. gibbosum* at approximately 3 d intervals. During 1986 censuses were conducted weekly. Newly discovered, unmarked, individuals were removed from the gorgonian colony; the shell was given a unique mark by scoring it with a triangular file (after Harvell & Suchanek 1987); and the snail returned to the gorgonian. Small *C. gibbosum* (< 1 cm in length) had shells which were too thin to score. These individuals were identified on the basis of their size and location.

Preferences were assessed by comparing the distribution of *Cyphoma gibbosum* on gorgonians to gorgonian species abundances (numbers of colonies). Comparisons were made using *G*-tests (Sokal & Rohlf

1969). Where possible, data for each year were divided into months and also analyzed for differences between months (temporal heterogeneity). In one case (Macaroon), where there were many observations of marked individuals, the data were also analyzed for different preferences among snails. Large numbers of empty cells weaken the accuracy of this one test. In all other tests empty cells and cells with fewer than 5 observations were pooled to increase accuracy.

The preferences of individual snails were assessed by determining if the snail was observed a majority of the time on a single species. A snail present on one species more than 50% of the times it was observed was considered to have a preference. Snails which only were observed on a single occasion were excluded from this analysis. The numbers of snails preferring different gorgonian species were then compared to gorgonian abundances with *G*-tests.

The data were also analyzed for clumping of snails and for associations between individual snails. Clumping was determined by comparing the distributions of numbers of snails on individual colonies to that expected from Poisson distributions of snails. The mean probability of a snail occupying a colony was determined using only colonies which were occupied at some time during the study. This eliminates bias introduced if certain colonies were avoided by snails. The analysis was made even more conservative by excluding deviations in the numbers of colonies without snails. This procedure tests the hypothesis that snails were distributed randomly among the 'acceptable' colonies, where acceptable colonies are those which were visited at least once.

Associations were determined by calculating the proportion of censuses in which 2 snails were observed together. The index is defined by:

$$A_{1,2} = O_{1,2} / O_{\max}$$

where  $O_{1,2}$  = number of times Snail 1 was observed with Snail 2;  $O_{\max}$  = total number of observations of either Snail 1 or 2, whichever is the greater of the two. Associations were considered 'significant' when *A* was greater than 0.5.

Preferences at other sites in the Caribbean were determined from the distribution of snails among 200 randomly chosen colonies. The number of snails present on each colony was recorded and their distribution compared to the relative abundances of the gorgonian species using *G*-tests. Surveys on St. Croix, US Virgin Islands, and Puerto Rico were conducted in August and December 1986 respectively, and surveys on Aruba and Bonaire, Netherlands Antilles, were conducted in January 1987. A similar set of surveys was also conducted at the 3 San Blas sites in May 1987. For com-

parative purposes semiweekly censuses were also made at the San Blas sites during May 1987.

## RESULTS

### Population fluctuations

*Cyphoma gibbosum* was common at all 3 San Blas sites, but densities varied between sites and years (Table 1). At Macaroon the greatest numbers of snails were discovered during the June–July 1986 censuses. Similar densities were observed in April 1985. The disparity between mean densities and the total number of individuals identified during each of the census periods indicates that only some of the snails in the population were present in any one census (52 to 98%). Seven of the individuals marked in 1984 (18.8% of the population) were also observed in 1985, and one of those snails was again observed in 1986. Six of the snails marked in 1985 (9% of the population) were observed in 1986.

Mortality in which marked shells were recovered was restricted to 1 snail in 1984, 3 in 1985 and 1 in 1986. Two of the recovered shells were whole; 2 other shells exhibited damage along the lip which may have been caused by a crab; and the fifth was almost completely crushed but deposited in one location. Based on these data the per capita mortality rate was  $0.016 \text{ mo}^{-1}$  ( $19.7\% \text{ yr}^{-1}$ ) in 1984 and 1985, and  $0.013 \text{ mo}^{-1}$  ( $15.6\% \text{ yr}^{-1}$ ) in 1986. These mortality estimates exclude cases in which an individual was killed outside of the study area as well as cases in which the shell was totally destroyed. Several empty unmarked shells were also collected from the Macaroon site in 1985 and 1986. Of these 10 additional shells, 4 were undamaged, 2 had the shell aperture broken and 4 exhibited a small uneven hole like that expected from stomatopod predation.

On average *Cyphoma gibbosum* was least common at Korbiski. *C. gibbosum* densities were similar for the summer months of 1983 to 1985, but densities increased sharply in January 1984 and again in June 1986. *C. gibbosum* is regularly collected by children from the surrounding islands and used to make necklaces which are sold to tourists. The Korbiski site is the shallowest and most accessible of the 3 sites, and as such is the most likely to be affected by human activities. Therefore, collecting pressure must be considered as a possible cause of population fluctuations at Korbiski. However, the population fluctuations at Korbiski were similar to those observed at Pinnacles, a more isolated site. Four of the 10 snails labelled in 1984 were also present at the site in 1985. There were no recoveries of empty labelled shells at Korbiski.

Table 1. *Cyphoma gibbosum*. Density (number 100m<sup>-2</sup>) at 3 sites in the San Blas Is., Panama

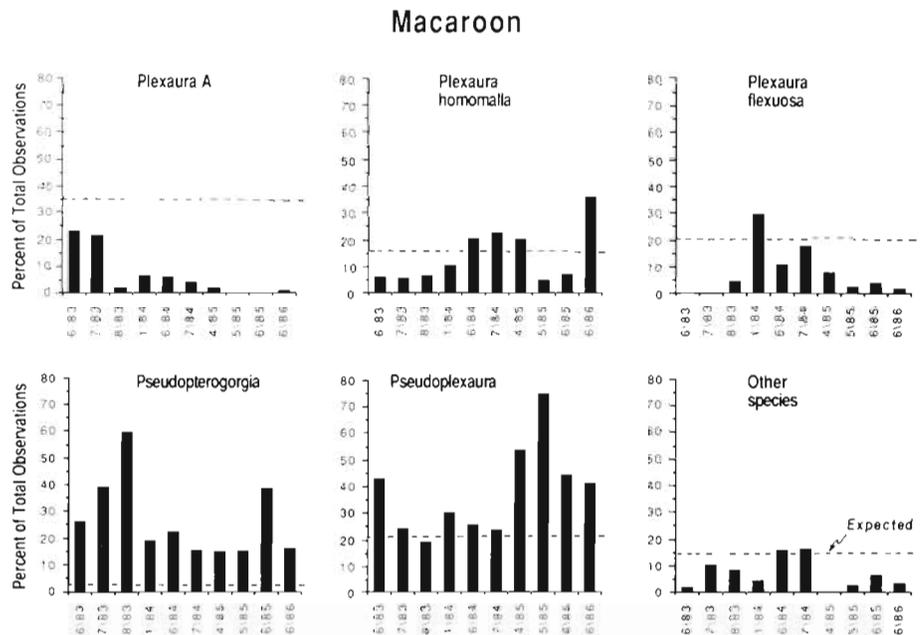
Census period	Mean density	Standard error	No. of days censused	No. of individuals identified	Total no. of observations
<b>Macaroon</b>					
1983 June	6.8	0.8	8	NA	52
July	10.0	2.0	4	NA	38
August	16.0	3.0	3	NA	48
1984 January	23.5	0.5	2	NA	47
June	15.7	2.4	6	30	159
July	24.8	0.8	10	28	228
August	22.5	0.5	2	23	
1985 April	27.9	1.2	13	48	357
May	20.4	0.7	9	37	184
June	16.0	1.1	8	26	128
1986 June–July	27.9	1.5	7	55	195
<b>Korbiski</b>					
1981 July	2.4	0.4	16	NA	36
1983 June	2.3	0.2	13	NA	30
July	3.8	0.4	8	NA	30
August	5.1	0.3	8	NA	35
1984 January	15	1.0	2	NA	30
June	3	0.3	6	4	18
July	4.4	0.2	10	5	43
August	1.5	0.5	2	2	
1985 April	6.9	0.6	7	10	42
May	5.4	0.5	11	10	50
June	3.3	0.5	8	5	25
1986 June–July	10.9	0.8	7	20	79
<b>Pinnacles</b>					
1984 June	6.8	0.6	6	10	58
July	7.5	0.6	10	9	74
August	8.0	0.7	2	9	
1985 April	16.0	0.9	7	23	112
May	17.1	0.6	10	29	171
June	16.0	0.5	9	29	144
1986 June–July	2.7	0.6	7	5	19
NA: data not available					

As at Korbiski *Cyphoma gibbosum* abundances at Pinnacles varied markedly between years. The cause of the dramatic drop in abundance in 1986 is unknown. Four of the snails marked in 1984 (28.6% of the population) were observed again in 1985. None of the previously marked snails were found in 1986. Mortality rates based on the collections of marked empty shells were 0.0 mo<sup>-1</sup> in 1984, 0.019 mo<sup>-1</sup> in 1985 and 0.0 mo<sup>-1</sup> in 1986. In addition to *C. gibbosum* 3 individuals of *Cyphoma signatum* were observed at Pinnacles in 1984, 2 in 1985 and 1 in 1986. One of the 2 *C. signatum* observed in 1985 was marked in 1984. *C. signatum* were only observed on *Plexaurella* spp.

### Species preferences

*Cyphoma gibbosum* distribution patterns are generated by 2 independent processes: the movement of individuals to colonies and the time spent on a colony once a choice has been made. In a detailed analysis of the 1984–1986 San Blas data (Lasker et al. 1988) we have shown that in their movements (choice of which colony to move to) *C. gibbosum* regularly displayed preferences for *Pseudopterogorgia* spp., *Plexaura homomalla* and *Pseudopterogorgia* spp. Similar results were observed in the amount of time a snail remained on colonies of the different species (Lasker et al. 1988).

Fig. 1. *Cyphoma gibbosum*. Distribution on gorgonians at Macaroon Reef, San Blas Is., Panama. Distributions for each month are depicted as the percentage of the total number of observations for that month. Total number of observations for the month is listed in Table 1. Predicted value (dashed line) is based on the relative number of colonies measured in 1983. (Variation in the abundance of the gorgonians over time at these sites was minimal)



In concert, movement and length of stay generated distribution patterns which displayed a strong bias toward *Pseudopterogorgia* colonies and positive but lesser preferences for *P. homomalla* and *Pseudoplexaura* spp. colonies. Although those trends were evident at all 3 San Blas sites, there was considerable temporal variation in the degree of preference as well as variation between sites. In this section we examine the source of variation at each of the San Blas sites.

Since different individuals were present in the study area at different times, the presence of individual host preferences also introduced temporal variability in the data. Individual snails were not marked in 1983, but the sudden appearance of snails on a single *Pseudopterogorgia americana* colony in August 1983 suggests that individual preferences created the significant tem-

Macaroon

**Individual preferences.** *Cyphoma gibbosum* distributions at Macaroon are presented in Fig. 1. When compared to colony abundances, *Pseudopterogorgia* spp. were the most preferred species, always followed in preference by *Plexaura homomalla* or *Pseudoplexaura* spp. Monthly variation in distribution patterns was attributable to differences in the preferences of individual snails. In 1984, 36 of the 38 snails exhibited a preference for a single gorgonian species. The numbers of snails preferring each host species were not distributed randomly with respect to species abundance ( $G = 233.7$ ,  $df = 5$ ,  $p < 0.005$ ). When corrected for colony abundance *Pseudopterogorgia* spp. followed by *P. homomalla* were the most preferred species (Fig. 2). In 1985, 59 of the 61 snails had identifiable preferences, and *Pseudopterogorgia* spp. were again the most preferred species ( $G = 50.6$ ,  $df = 3$ ,  $p < 0.003$ ). A similar pattern of non-random distribution of individual preferences ( $G = 71.88$ ,  $df = 4$ ,  $p < 0.001$ ) was observed in 1986. However, *P. homomalla* was the most commonly preferred species in 1986.

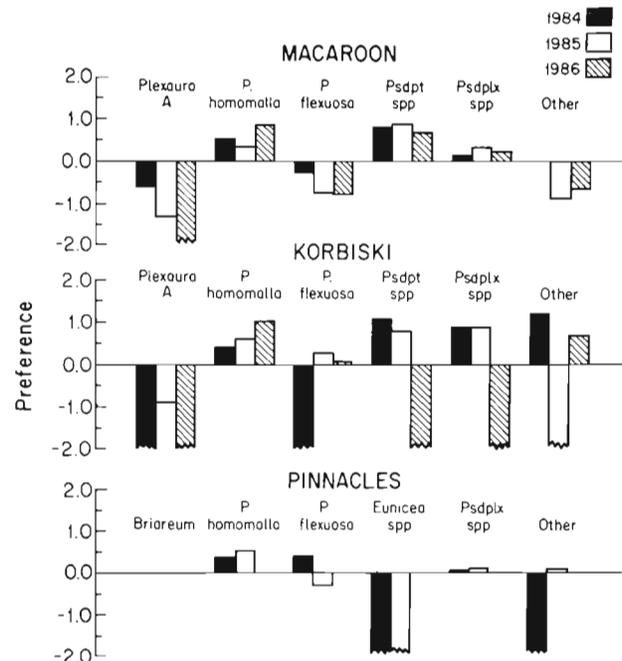


Fig. 2. Prey preference exhibited by individual snails at each of the 3 study reefs for 1984, 1985 and 1986. Number of snails preferring each of the species is depicted relative to gorgonian colony abundances. Preference = log (observed/expected)

poral heterogeneity in distribution patterns ( $G = 30.68$ ,  $df = 10$ ,  $p < 0.005$ ). In 1984 the data exhibited significant heterogeneity between snails ( $G = 1076.0$ ,  $df = 185$ ,  $p < 0.005$ ) as well as significant interactions between months and snails ( $G = 89.0$ ,  $df = 37$ ,  $p < 0.005$ ) and between host choice, month and snails ( $G = 662.6$ ,  $df = 185$ ,  $p < 0.005$ ). There was no significant interaction between host preference and months ( $G = 6.84$ ,  $df = 5$ ,  $p > 0.10$ ). During 1985 significant heterogeneity was found in the distribution data due to interactions between host and months ( $G = 89.7$ ,  $df = 10$ ,  $p < 0.005$ ) host and snails ( $G = 1296.4$ ,  $df = 300$ ,  $p < 0.005$ ), and snail and month ( $G = 480.8$ ,  $df = 120$ ,  $p < 0.005$ ). As in 1984 the significant interactions can be related to the preferences of individual snails and their pattern of appearance at the Macaroon study site.

The individual preferences displayed by snails were not static. Seven snails originally marked in 1984 were observed on multiple occasions in 1985. Only 2 of these snails exhibited the same preference in both years. In one case a snail was found exclusively on a single *Pseudoplexaura porosa* colony in both 1985 and 1986 (5 of 5 cases in 1986 and 26 of 26 in 1985).

**Clumping and associations.** Individual preferences and the variability of those preferences can be correlated with the presence of aggregations of snails on specific colonies. The formation and breakup of those aggregations created much of the variability in the data. *Cyphoma gibbosum* exhibited clumped, or aggregated, distributions on colonies at Macaroon (1984,  $G = 95.7$ ,  $df = 4$ ,  $p < 0.005$ ; 1985,  $G = 660.5$ ,  $df = 7$ ,  $p < 0.001$ ). This aggregative pattern was created by the consistent occupancy of certain individual

colonies which were often occupied by aggregations of snails in both 1984 and 1985. For instance, in 1984, 1 to 4 snails were always found on a single *Pseudopterogorgia americana* colony. In 1985 as many as 7 individuals were found on the same colony, and in May 1987, a year for which we have only limited census data, we observed as many as 28 individuals on that same colony.

Aggregations were not stable groupings of individual snails. This is evident in the level of association among the different snails. Only 3 groups of co-occurring snails were identified in the association analysis of the 1984 data. Two of the groups contained 3 snails each and the third group contained 2 snails. The group of 2 snails moved together, making 3 identical switches among colonies. Only 2 groups of snails (2 snails and 3 snails each) were identified in 1985. Each group predominantly occupied a single colony, but in neither of these groups were movements on and off of the colony coordinated. All other aggregations were created by the tendency of snails to move to and remain on colonies which already contained snails regardless of the individual identity of those snails.

#### Korbiski

**Individual preferences.** In all years except 1981, *Cyphoma gibbosum* preferred either *Pseudopterogorgia* spp., *Plexaura homomalla* or *Pseudoplexaura* spp. (Fig. 3). (In 1981 the presence of snails on a single *Gorgonia* sp. colony led to the apparent preference for *Gorgonia* spp. ['Other' in Fig. 3]. By 1983 the *Gorgonia*

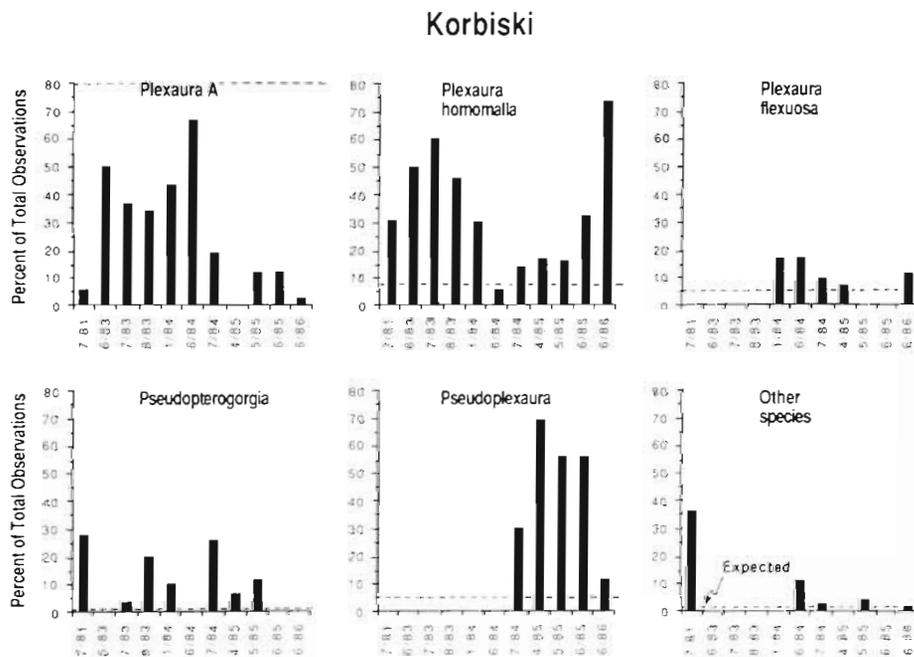


Fig. 3. *Cyphoma gibbosum*. Distribution on gorgonians at Korbiski Reef, San Blas Is. See Fig. 1 for full explanation

sp. colony which had been heavily grazed in 1981 had died.)

Variation in distribution patterns at Korbiski can be attributed to the pattern of appearance and disappearance of individual snails with different preferences and not to preferences and changes in behavior common to all snails. For example, of the 10 snails followed in 1984, 1 exhibited a clear preference for *Pseudopterogorgia americana*, 2 for *Pseudoplexaura porosa*, 1 for *Plexaura homomalla* and 1 for *Eunicea* spp. In 1985 disproportionate numbers of snails preferred *Pseudoplexaura* spp., *Pseudopterogorgia* spp., and *P. homomalla* colonies. *P. homomalla* was the most commonly preferred species in 1986, with 13 of the 20 snails preferring it. Preference for *Briareum asbestinum* ('Other' in Fig. 1) was observed in 1986 due to the presence of 2 snails which were often observed on a single *B. asbestinum* colony. The numbers of snails specializing on the different species were significantly different from that expected from a random distribution of preferences in 1985 and 1986 (1985,  $G = 6.23$ ,  $df = 1$ ,  $p < 0.025$ ; 1986,  $G = 72.11$ ,  $df = 1$ ,  $p < 0.001$ ). (The presence of only 5 snails with definable preferences in 1984 made it impossible to test for significant deviations from random expectations.) The almost total lack of specialization of individual snails on *Plexaura* A accounts for most of the deviation from random expectations. Four of the snails present at the Korbiski site in 1985 were originally observed in 1984. None of these individuals exhibited the same preferences as observed in 1984.

Individual preferences in concert with the pattern of appearance of different snails generated significant temporal heterogeneity in distribution patterns in both 1984 and 1985 (1984,  $G = 27.97$ ,  $df = 5$ ,  $p < 0.005$ ; 1985,  $G = 25.375$ ,  $df = 10$ ,  $p < 0.005$ ). Analysis of the 1983 data also reveals significant temporal heterogeneity in distributions ( $G = 11.99$ ,  $df = 4$ ,  $p < 0.025$ ). This heterogeneity was caused by occupancy of a single *Pseudopterogorgia americana* colony during late July and August. The lack of marked snails makes it impossible to determine the extent to which the temporal heterogeneity in 1983 reflected changing preferences or different preferences among separate snails.

**Clumping and associations.** The distribution of snails among colonies at Korbiski was also clumped. Snails were found sharing a colony with a second snail more often than expected (deviation from Poisson expectations; 1984,  $G = 6.00$ ,  $df = 2,22$ ,  $p < 0.05$ ; 1985,  $G = 105.4$ ,  $df = 4$ ,  $p < 0.005$ ). Groups of as many as 5 snails were observed together in 1985. The distribution pattern changed over the 3 mo of monitoring in 1985 creating significant temporal heterogeneity in clumping ( $G = 121.1$ ,  $df = 6$ ,  $p < 0.005$ ). Clumping was

greatest during April. No associations between snails were recognized in 1984. One group of 3 snails which moved between 2 *Pseudoplexaura porosa* colonies was detected in 1985.

As at Macaroon, species preferences were attributable to preferences for individual colonies. This was the case for *Pseudopterogorgia* in 1981, 1983, and 1984, and for *Pseudoplexaura porosa* in 1984. The 1985 preference for *P. porosa* colonies can be attributed to the preference of 4 snails for 2 adjacent colonies. These snails remained on or within several meters of the 2 colonies throughout the 3 mo sampling period.

### Pinnacles

**Individual preferences.** Most of the snails at Pinnacles exhibited strong individual preferences, which were not distributed among the species randomly (Fig. 2; 1984,  $G = 84.16$ ,  $df = 1$ ,  $p < 0.005$ ; 1985,  $G = 13.34$ ,  $df = 3$ ,  $p < 0.005$ ). In both 1984 and 1985 more snails than expected preferred *Plexaura homomalla* colonies and in 1984 more than expected preferred *P. flexuosa* (Fig. 2). Distribution patterns differed significantly between months during both years (Fig. 4; 1984,  $G = 37.598$ ,  $df = 5$ ,  $p < 0.005$ ; 1985,  $G = 38.64$ ,  $df = 10$ ,  $p < 0.005$ ). Individual preferences did not remain constant between years (Fig. 4). Four of the snails found in both 1984 and 1985 had definable preferences in both years, but of those only one maintained the same preference in both years.

**Clumping and associations.** The 1984 Pinnacles data are the only data which do not exhibit significant clumping of snails ( $G = 6.09$ ,  $df = 3$ ,  $p > 0.1$ ). Only 2 snails were found together over 50 % of the time. Those 2 spent most of their time on a single *Pseudoplexaura porosa* colony, but movements of the snails on and off the colony were not correlated. As at the other sites, in 1985 *Cyphoma gibbosum* were significantly clumped in their distribution ( $G = 221.3$ ,  $df = 4$ ,  $p < 0.005$ ). However, there was only a single pair of individuals which regularly co-occurred on the same colonies. This pair was only observed on a single colony which they twice left and returned to together.

### Geographic variation

The number of *Cyphoma gibbosum* observed at each of the other Caribbean sites, the species they were observed on, and the abundances of the most common gorgonians are listed in Table 2. Preferences were determined by comparing the number of snails found on the different species to that predicted by the binomial distribution. Significant deviations from the bino-

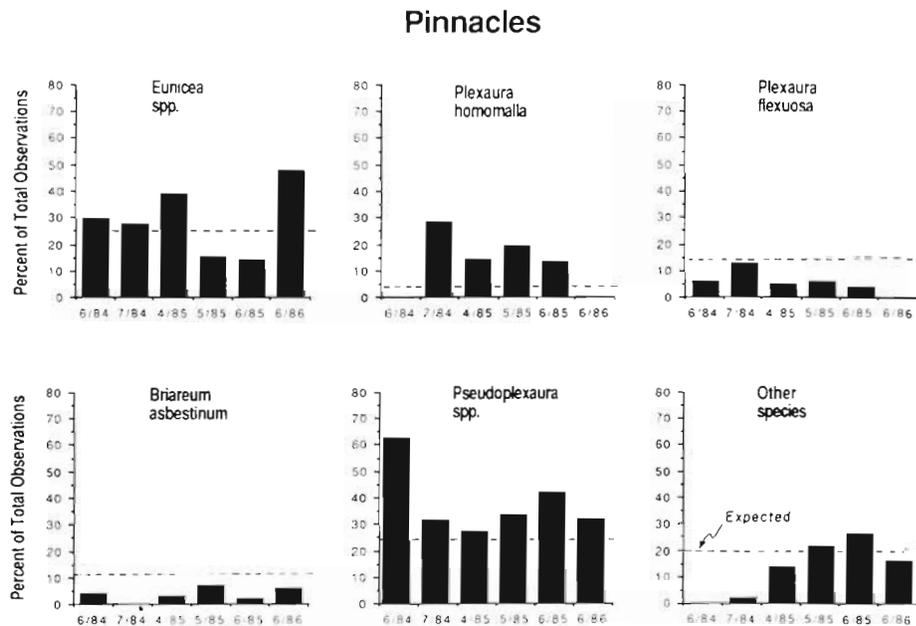


Fig. 4. *Cyphoma gibbosum*. Distribution on gorgonians at Pinnacles Reef, San Blas Is. See Fig. 1 for full explanation

mial prediction were observed at 8 of the 17 reefs. *Pseudopterogorgia* spp. were preferred colonies at 5 of those reefs. Similar surveys conducted at the 3 San Blas sites are also included in Table 2. Using this sampling procedure we were only able to detect a preference for *Plexaura homomalla* at Korbiski. The relative abundance of *C. gibbosum* at the 3 San Blas sites was very similar to that determined from censuses of the 100 m<sup>2</sup> sites (mean of 5 censuses in May 1987; 4.9, 4.8, 23.6 at Macaroon, Pinnacles and Korbiski respectively).

## DISCUSSION

*Cyphoma gibbosum* preferences observed in this study varied considerably among individuals, sites and times. A total of 8 different genera or species were identified as preferred at the different sites and at different times. The group most commonly identified as preferred was *Pseudopterogorgia* spp. A number of other studies have also found preferences for *Pseudopterogorgia*, specifically *Pseudopterogorgia americana* (Birkeland & Gregory 1975, Yoshioka 1979, Harvell & Suchanek 1987). Thus the preference for *Pseudopterogorgia* colonies appears to be consistent both temporally and geographically. But what of individual snails which preferred other species and of sites at which different preferences were observed? Are these cases of true variation or are they cases of sampling error generated by insufficient sampling?

There are several striking differences among the preferences reported from different locations. For in-

stance, Birkeland & Gregory (1975) found that *Gorgonia* spp. along with *Pseudopterogorgia americana* made up a greater portion of *Cyphoma gibbosum* diets than expected on the basis of colony abundance. In contrast *Gorgonia* spp. was preferred at our study sites in only a single year and at a single site. Our only San Blas observations of *C. gibbosum* on *Gorgonia* were restricted to a single colony at Macaroon. Although we observed *C. gibbosum* on *Gorgonia* colonies at some of our other Caribbean sites, the use of *Gorgonia* colonies at those reefs did not approach that described by Birkeland & Gregory (1975) for both Lameshur Bay St. John, US Virgin Islands, and Galeta Islands, Panama.

A similar discrepancy in preference may also occur in the use of *Briareum asbestinum* colonies. Hazlett & Bach (1982) did not assess host preferences in their study of *Cyphoma gibbosum* at Hull Bay, St. Thomas, US Virgin Islands, but their study implies that *B. asbestinum* was the most commonly occupied gorgonian at their study site. We also have observed *C. gibbosum* on *B. asbestinum* at sites in which *B. asbestinum* was common (Puerto Rico and Virgin Gorda, British Virgin Islands). In the San Blas we found a preference for *B. asbestinum* at Korbiski in 1986 which involved a group of 2 snails and a single colony. Similarly, we encountered a significant preference for *B. asbestinum* at Corona de Laurel in Puerto Rico (Table 2). At other times and at all of the other sites as well as at Lameshur Bay (Birkeland & Gregory 1978) *B. asbestinum* were occupied less often than predicted on the basis of abundance.

There also were many inconsistencies in the level of

Table 2. *Cyphoma gibbosum*. Number observed at different sites in the Caribbean and relative abundance of the most common gorgonians. Values are presented as number of *C. gibbosum*/ % gorgonian abundance (only % gorgonian abundance is presented for sites in which *C. gibbosum* was not observed). Only data on common or heavily utilized gorgonian species are presented. Thus percent abundances from any single site do not always add to 100. BA: *Briareum asbestinum*; EU: *Eunicea* spp.; GO: *Gorgonia* spp., PH: *Plexaura homomalla* forma *homomalla*; PHK: *P. homomalla* forma *kükenthali*; PSD: *Pseudoplexaura* spp.; PST: *Pseudopterogorgia* spp.

Location	Species							Other preferred species
	BA	EU	GO	PH	PHK	PSD	PST	
Aruba, Netherlands Antilles								
Refinery reef	0	34	1	1	1	1	6/18*	
Bonaire, Netherlands Antilles								
Alice-in-Wonderland	4/21	5/15	0	2/9	5	5/31	4/10*	
Karpata	21	14	2	1/27	5	1/14	1/4	
Jerry's Jam	0	0	0	78	0	0	0	
Pink Sand Beach	0	13	0	5	0	1/19	4/21	
Windjammer Wreck	3	0	0	34	0	3/23	6	
Puerto Rico								
Corona Blanca	2	3	2	1	0	2/10	3/82	3/2* ( <i>Plexaurella</i> sp.)
Corona de Laurel	3/3	5/31*	4	0	3	6	41	
Enrique	3	12	8	1	0	1/3	38	
La Gata	1	11	7	3	0	14	2/22*	
La India	1	21	3	4	2	10	10	
Site 2	6	2/11	4	4	9	14	2/29	
St. Croix, USVI								
Buck Is.	42	1	0	7	11	1/33	0	16/25* ( <i>Muriceopsis</i> sp.)
Coakley Bay	0	3	2	3/14	0	2/29	0	
Porpoise Point (8 m)	0	2/19	9	6	4	7/40	4/3*	
Porpoise Point (15 m)	1/8	0	7	11	6	3/42	1	
Tague Bay (forereef patches)	1/5	10	5	11	8	28	9/6*	
St. John's USVI <sup>a</sup>								
Lameshur Bay	16	1	6	--	5	25 <sup>b</sup>	6	
San Blas Islands, Panama								
Macaroon	1	1/4	0	12/15	0	17/36	2/4	
Pinnacles	7	15	3	5	0	2/36	4	
Korbiski	0	3	0	12/11	0	3/14	6	

\* Significantly more snails than expected by binomial probabilities,  $p < 0.05$

<sup>a</sup> Birkeland & Gregory (1975)

<sup>b</sup> *Pseudoplexaura flagellosa*

preference among other species, but some of these differences may be explained by differences in abundances of these species at the different sites. *Pseudoplexaura* spp., a common species in the San Blas, were among the species preferred there. However, they were not preferred at the other Caribbean sites which we examined, nor were they preferred at either Salt River Canyon, St. Croix (Harvell & Suchanek 1987) or Lameshur Bay (Birkeland & Gregory 1975). The lack of preferred use of *Pseudoplexaura* at these sites may be generated by low species abundance in concert with differing preferences for the different *Pseudoplexaura* species. The *Pseudoplexaura* spp. category which we report as a preferred group in the San Blas was dominated by *P. porosa*. However, Birkeland & Gregory (1975) only report the presence of *Pseudoplexaura*

*flagellosa*. (*P. porosa* at Lameshur Bay were presumably included in Birkeland & Gregory's 'Other gorgonaceans' category.) Similarly, *P. porosa* was less common at the Puerto Rico sites than in the San Blas.

*Plexaura homomalla*, another preferred San Blas species, was present in low to intermediate densities at all of the sites, but varied tremendously in the degree to which it was occupied by *Cyphoma gibbosum*. In this case differences in the relative abundance of the different forms of *P. homomalla* may explain some of the variation in the distribution patterns. *P. homomalla* forma *homomalla* was the only form of *P. homomalla* in the San Blas. However, in Puerto Rico and St. Croix, where *P. homomalla* was not preferred, *P. h. homomalla* was much less common than in the San Blas. Furthermore, *P. homomalla* forma *kükenthali*

which made up about half of the *P. homomalla* population at the Puerto Rico and St. Croix sites is avoided by *C. gibbosum* (Table 2 and Birkeland & Gregory 1975).

The variation between sites, years, and individuals may best be interpreted as an interaction between the aggregative behavior of *Cyphoma gibbosum* and differing levels of preference. Firstly, much of the variation in preferences can be attributed to social interactions between individual snails. *C. gibbosum* were distributed on colonies in an aggregated manner and were more likely to visit and remain on a colony if another snail was also present (Gerhart 1986, Lasker et al. 1988). At any one site this aggregative behavior produced a distribution pattern in which a small number of colonies were heavily utilized. Gerhart (1986) has suggested that these aggregations are generated by the tendency for *C. gibbosum* to follow the mucous trails of other individuals. His hypothesis is consistent with the aggregations which we observed as well as the fact that aggregations are not made up of groups of individuals which always travel together. Trail-following reinforces choices made by 'lead' snails and thereby reinforces preferences, but the behavior also magnifies the effects of an individual choosing a 'non-preferred' species. When only 1 or 2 aggregations are observed the trail-following behavior could create spurious species preferences. This bias is a serious concern in those data sets in which the species preference was created by occupancy of a single colony, a phenomenon which frequently occurred in the *Pseudopterogorgia* data. The tendency for individuals to become entrained on a single colony or among a small group of colonies also may account for the apparent changes in the preferences of individual snails. Given this behavior, species preferences only become apparent in the repetition of the preference among many individuals and/or among different sites and in different years.

The second factor which contributes to the observed variation in distribution patterns is the existence of preferences for different prey species. We propose gorgonian species may fall into 1 of 3 classes, unacceptable, acceptable and preferred. At this time the only species which unambiguously fall in the preferred category are *Pseudopterogorgia* spp. (primarily *P. americana*). *Pseudopterogorgia* colonies were preferentially used by *Cyphoma gibbosum* at a wide variety of sites. This preference is clearest in the large multi-year data sets. The other readily distinguished gorgonians are the unacceptable species. Perhaps the best examples of this group are the plexaurids *Plexaura A* and *Plexaura homomalla* forma *kükenthalli*. These species were grossly under-utilized by *C. gibbosum* even when they were among the most abundant gorgonian species. The final group is made up of acceptable

species. These are the species which snails choose in a random fashion and then finding them acceptable remain on them. The tendency for individuals to aggregate magnifies what may be initially random choices and creates the appearance of a preference. The more common these species are, the greater the subsequent skew from random distribution patterns. The apparent preference for *Pseudoplexaura* spp. was probably enhanced by this effect. *Pseudoplexaura* colonies were regularly occupied at many of the sites and tended to be sites of preferential occupancy in those localities in which they were particularly abundant. *P. homomalla* forma *homomalla*, *Gorgonia* spp., *Briareum asbestinum* and *Muriceopsis* also may fall into this group. (*Muriceopsis* sp. was virtually absent at all of the other sites which leaves open the possibility that it is a preferred species). Preferential use of abundant species could also occur if snails become entrained on the more frequently occupied prey species. Such an effect has been observed in the feeding behavior of the nudibranch *Aeolidia papillosa* (Hall et al. 1982).

*Cyphoma gibbosum* behavior is illustrative of the complexity involved in defining 'prey choice'. *C. gibbosum* exhibited clear preference for *Pseudopterogorgia* spp. This preference as well as that for additional species probably is related to differences in the quality of gorgonians as food sources and as habitats in which to live (Lasker et al. 1988). Some of the variation in preferences may be attributable to heterogeneity within the gorgonian taxa, such as that seen between the forms of *Plexaura homomalla*. Overlaying those preferences and perhaps obscuring them are the observations that at any one moment in time individuals exhibited choices which varied from the group mean. Much of this variability may be related to social behaviors which led to the formation of aggregations.

These findings have several important consequences for the investigation and interpretation of preference among grazers like *Cyphoma gibbosum*. Firstly, social interactions can generate the appearance of preferences. These 'preferences' are not necessarily indicative of differences in the prey themselves and are artifacts of stochastic choices and interactions among the grazers. Only monitoring of large numbers of grazers over time and/or across sites will distinguish between these processes and preferences based on characteristics of the prey species. Secondly, although the processes generating the 'choices' include stochastic factors, the resultant damage is as important to the prey as that which occurs when a colony is chosen for some other reason. Among communities in which some colonies are chosen because of their abundance, grazing will vary temporally and spatially, as prey abundances change. It is therefore essential to understand

the basis on which prey choices are made before predicting the long-term effects on prey community structure. Finally, although they are more difficult to discern, preferences based on species and colony-specific differences among prey play an important role in the activity of the grazer and its effects on the community. However, we again note that it may not be possible to seek deterministic explanations for each observation of preferential feeding.

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